LRH: Norghauer

RRH: Vine Colonization of Seedlings in Gaps

Insects and light interact to mediate vine colonization of fast-growing *Microberlinia bisulcata* tree seedlings in gaps of an African rainforest

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ABSTRACT

Vines thrive in lowland tropical forests yet the biotic factors underlying their colonization of host tree seedlings and saplings remain surprisingly understudied. Insect herbivores presumably could influence this process, especially where disturbance has opened the canopy (i.e., gaps)—temporary areas of higher primary productivity favoring the recruitment of vines and trees and invertebrates in forests—but their impact on vine colonization has never been experimentally tested. Using data from an insect-herbivore exclusion (mesh-netting cages) experiment conducted in an African rainforest (Korup, Cameroon), I logistically modeled the probability of vines colonizing seedlings of three co-dominant species (*Microberlinia bisulcata* vs. *Tetraberlinia bifoliolata* and *T. korupensis*) in paired shaded understory and sunny gap locations (41 blocks across 80 ha, n = 664 seedlings) in a 1–2-yr period (2008–2009). Vine colonization occurred almost exclusively in gaps, occurring on 16% of seedlings there. Excluding herbivores in gaps doubled colonization of the light-demanding and faster-growing *M. bisulcata* but had negligible effects on the two shade-tolerant, slower-growing and less palatable *Tetraberlinia* species, which together were twice as susceptible to vines under natural forest gap conditions (controls). When protected from herbivores in gaps, more light to individual seedlings strongly increased vine colonization of *M. bisulcata* whereas its well-lit control individuals supported significantly fewer vines. These results suggest vines preferably colonize taller seedlings, and because light-demanding tree species grow faster in height with more light, they are more prone to being colonized in gaps; however, insect herbivores can mediate this process by stunting fast-growing individuals so that colonization rates becomes more similar between co-occurring slow and fast growing tree species. Further influencing this process might be associational resistance or susceptibility to herbivores linked to host species' leaf traits conferring shade-tolerance ability

as seedlings or saplings. A richer understanding of how vines differentially influence forest regeneration and species composition may come from investigating vine–tree–herbivore interactions across light gradients, ideally via long-term studies and intercontinental comparisons.

Key words: forest ecology; gap-phase regeneration; herbivory; light-demanding tree species; plant-insect interactions; treefall gaps; tropical forest; vines

CLIMBING PLANTS (VINES) ATTAIN THEIR GREATEST BIOMASS, ABUNDANCE, AND DIVERSITY in lowland tropical forests, where they figure prominently in the structure, composition, and dynamics of these species-rich communities (Gentry & Dodson 1987; Richards 1996; Schnitzer & Bongers 2002). Nevertheless, biogeographically, vine abundance varied almost 10-fold among 30 pantropical forest sites in relation to climate, with the highest vine diversity (Fisher's alpha) currently found in the central African rainforest of Korup National Park (DeWalt et al. 2015). In using neighboring plants for structural support, vines hinder the growth of their host trees (Putz 1984; Schnitzer & Carson 2010; reviewed by Marshall et al. 2017), which, by altering recruitment rates in to the canopy, could influence the composition of vegetation recovering from disturbance (Barry et al. 2015) and host-population dynamics, especially of faster-growing, light-demanding tree species whose vine loads can greatly decrease their per capita survival rates (Visser et al. 2018a). But despite early calls (Clark & Clark 1990 [p. 329]), we still know little of the factors influencing young vines' attachment to very young trees (hereafter 'vine colonization'). This interaction should be studied because not only are tree seedlings abundant, they are also highly vulnerable to mortality yet strongly limited in growth by attenuated light resources (Richards 1996). Both factors may be exacerbated by having to support vines whose leaves would interfere with host plant capture of already scarce light near the forest floor; this

would not only reduce growth but also could push seedlings of some species below their light-compensation points (Perez-Salicrup 2001; Toledo-Aceves & Swaine 2008a,b). In short, vines may function as a biotic stress factor in the key seedling-to-sapling life stage transition in forests.

For most vines, their abundance and diversity in tropical forests is enhanced by disturbances that open the canopy (Richards 1996; Schnitzer & Bongers 2002), whether from logging or natural tree deaths and large branch-falls (Putz 1984; Babweteera et al. 2000; Schnitzer & Carson 2001; Marshal et al. 2017). It is in such treefall or canopy gaps—long recognized as a prominent feature of tropical forests influencing their turnover and species distributions (Denslow 1987)—that vines often aggregate and proliferate (Dalling et al. 2012; Piiroinen et al. 2013), presumably benefiting from not only more light for germination and growth (Richards 1996), but also more suitable growing support trees to climb onto than available in surrounding shaded forest (Putz 1984). A long history of removal experiments show that vines negatively affect multiple dimensions of tree regeneration, including hosts' access to water and light, growth and reproduction, and survival (reviewed by Estrada-Villegas & Schnitzer 2018), but this impact may depend on the local light environment as well as the shade-tolerance and species identity of hosts (Schnitzer & Carson 2010; Perez-Salicrup 2001; Toledo-Aceves & Swaine 2008a,b). From a young vine's perspective, locating a suitable support—one that increases its probability of survival or its growth rate—is arguably critical for its recruitment (Gianoli 2015), so colonizing taller, vigorously growing tree seedlings and saplings in gaps should be favored, because these hosts would offer more stable support and access to more light resources than slower-growing ones. Conspicuously missing, however, from this burgeoning research on vine–tree interactions is the involvement of herbivores, especially invertebrates.

A hypothesized role for herbivores in the interaction between regenerating vines and young trees in gaps is tenable for several reasons. Firstly, the greater light in gap habitats stimulates plant growth (Denslow 1987), and this sustained production of vegetation can strongly structure invertebrate communities (e.g., Perry et al. 2018), especially when serving as high-quality food (young stem and leaf tissues) that support higher insect herbivore densities and rates of folivory—hereon, "herbivore pressure"—than in the understory (Richards & Coley 2007, 2008). Secondly, leaf herbivory can differentially suppress and limit the stature of potential host tree species (in height or leaf area), especially if they lack sufficient resistance, or fail to compensate for eaten tissues, or cannot escape discovery by density-dependent natural enemies (Pearson et al. 2003; Marquis 2005; Massey et al. 2006; Norghauer et al. 2008; Norghauer & Newbery 2014; Lemoine et al. 2017). If vines can distinguish among and grow towards dark, shaded areas cast by very small stems (< 1-cm) of taller seedlings with more leaves, not unlike the skototropism demonstrated for root-climbers of buttressed tropical trees (Strong & Ray 1975) and other hosts (Gianoli 2015), then herbivory could reduce host susceptibility to vine colonization in gaps. Thirdly, although vines can compete with their hosts for light and belowground resources (Schnitzer et al. 2005; Toledo-Aceves & Swaine 2008a,b; Alvarez-Cansino et al. 2015), there is evidence from temperate systems of associational effects benefiting the fitness of the vine (Gonzalez-Tueber & Gianoli 2008) or host plant (Sasal & Suarez 2011). Fourthly, co-occurring vine and tree species likely share similar life-history tradeoffs soon after establishment (Gilbert et al. 2006), and that plant species identity and associated functional traits strongly influence susceptibility to herbivory is now well supported (Endara & Coley 2011). The fact, moreover, that globally tropical vines generally have lower leaf mass per area (LMA), lower foliar defenses (phenolics) and higher nitrogen and phosphorus per leaf mass than trees

(reviewed by Wyka et al. 2013) probably makes them particularly palatable to insects in gaps, which also might influence their ability to find and colonize host trees. Lastly, the high quantity of light (hereon, "light availability") reaching the forest floor in gaps is not uniform within and among them (Denslow 1987). Even small spatial differences in light may introduce further variation in plant growth rates and anti-herbivore defenses (Dudt & Shure 1994). This may affect not only host stature and vine foraging behavior reliant on such associated cues (Strong & Ray 1975, Gianoli 2015) but vines' own exposure to herbivory as well (Aide & Zimmerman 1990).

Another reason to study current plant-animal species interactions is to better predict implications of climate change. Dale et al. (2001) warned that the frequency, intensity, and duration of forest disturbances would likely be altered by climatic changes, driving shifts in the dynamics of forest ecosystems and their future composition. There is evidence that such projected increases in drought events are already hastening tree mortality (Allen et al. 2010). This, in combination with conditions favoring severe storms (hurricanes, windstorms; Dale et al. 2001), should generate more canopy-disturbed areas, including treefall gap formations; but since they tolerate drought better than trees, both factors are predicted to augment the abundance of vines (Schnitzer & Bongers 2011). Hence, interactions between vines, their hosts, and insects that eat them may strengthen over time, becoming increasingly crucial during gap-phase tree regeneration for structuring the community composition of tropical forests.

After reviewing the literature, I could not find any field studies that have attempted to experimentally quantify how herbivores influence the colonization of tree seedlings by vines. Marquis (2005) also noted this absence, "No studies are available that test the impacts of herbivores on vine colonization of their support hosts" (p. 336). Since then, a recent check did not list any such experimental vine–tree–herbivore studies in the database of

139 http://www.lianaecologyproject.com. Given the ubiquity of vines, insects, and seedlings in
140 tropical forests, their possible three-way interaction deserves some investigation by ecologists
141 and foresters alike. Here, I used data available from a large field experiment that excluded
142 insects from seedlings of three canopy tree species in a central African rainforest, analyzed at the
143 genus level (two shade tolerant congeners vs. a long-lived, light-demanding species), to test three
144 predictions: (1) Vine colonization increases with light availability to tree seedling hosts; (2) Tree
145 species with contrasting maximal growth rates (slow vs. fast) differ in their probability of being
146 colonized by vines in light-rich patches of forest (i.e., canopy gaps); (3) By equalizing host
147 species' stature (height, leaf area), insect herbivore pressure on tree seedlings interferes with the
148 vine colonization process in these gaps.

149 **METHODS**

150 FIELD HERBIVORE-EXCLUSION EXPERIMENT—The data came from primary lowland rainforest on
151 nutrient-poor soil, in Korup National Park, Cameroon, in the 82.5-h permanent "P-plot"
152 established in 1991 (Newbery et al. 1998, 2013). Briefly, the experiment had a fully crossed
153 factorial design—canopy cover × herbivory treatments—tested on three ectomycorrhizal,
154 masting tree species: one fast-growing (*Microberlina bisulcata* A. Chev) and two slow-growing
155 (*Tetraberlinia bifoliolata* Harms [Haumann], *Tetraberlinia korupensis* Weiringa) of contrasting
156 shade-tolerance in the Fabaceae subfamily Caesalpinioideae (Newbery et al. 2006). A total of n =
157 664 newly established seedlings (replicates, 13.5 to 32.3 cm tall) were physically protected from
158 insects (caged treatment) or accessible to them (control) in shaded understory and sunny gap
159 locations (= 41 blocks). Starting sample sizes and seedling heights are given in Table S1, with
160 more details found in Norghauer & Newbery (2013). A cage had sides of mesh netting with 1-
161 mm × 4-mm holes and its initial dimensions (W × L × H, all in cm) were c. 40 × 40 × 50, while

the control consisted of only a mesh rooftop (50 × 50) with open sides, likewise supported by four bamboo posts. Leaf litter on the control and cage structures was removed regularly during the experiment's duration (every 5–7 days, returned under rooftops of control and into the cages). To accommodate the growing seedlings in gaps, cages there were enlarged 1–3 times, as needed, to one or more dimensions: 50 × 50 × 75 or 100, 75 × 75 × 100 or 150, or 100 × 100 × 150 or 200; each time, its nearest control of the same species was similarly enlarged (i.e., given the same roof-top area of mesh; Norghauer & Newbery 2014). The mesh worked well at deterring herbivory from medium-sized insects: generally, throughout the experiment the caged seedlings had median values of 0–5% for leaf area eaten (refer to Table 3, Fig. 3,4 in Norghauer & Newbery 2013). Still, the experiment had several unavoidable limitations: namely, mammals were also excluded from cages; apart from the vines that germinated in cages, the entry or exit of other vines was likely impeded by the walled mesh netting—tendrils would have pass through the 4-mm^2 holes—whereas they could do so more easily under the control rooftop; and lastly, the bamboo frame of controls and cages may have drawn vines towards them.

LIGHT MEASUREMENTS—The amount of light reaching each seedling was directly quantified halfway through the experiment, in mid November 2008, under overcast conditions (Norghauer & Newbery 2013). To do this, at 1 m above each seedling (or higher for some larger individuals) a quantum photon sensor (model SKP215, Skye Instruments, Powys, UK) was placed and leveled to record the incident photosynthetic photon flux density (PPFD); at the same time, PPFD was recorded by a second sensor (same model type) positioned above the forest canopy (at ca. 0.5 km from the P-plot). Both sets of instantaneous measurements were made over a 1-week period (15–21 November, 2008). This rapid approach to determine light availability, developed by Messier & Puttonen (1995), was used because in other forests such diffuse light readings,

185 when expressed as percentage of above-canopy PPFD, are strongly correlated with mean daily
186 percent PPFD values in the understory (Comeau et al. 1998; Machado & Reich 1999).
187 VINE DATA RECORDED—The herbivore exclusion experiment had been installed over a 1-month
188 period (mid December 2007 to mid January 2008), which represented the *first census* when
189 starting plant sizes were measured; after ca. 22 months the mesh cages and rooftops were
190 removed from all tree seedlings (refer to Fig. 1 in Norghauer & Newbery 2013). Vine data for
191 experimental seedlings in gaps was obtained from the *third and fourth censuses only*, as detailed
192 below. At the start of the experiment, all seedlings (Table S1) were free of vines.
193 In the second census (mid November 2008), this initial sample of 664 experimental
194 seedlings was increased to 706 by adding 'replacements', primarily to offset sample size
195 reductions to rodents' lethally felled seedlings (Norghauer et al. 2016): for *M. bisulcata*: 32
196 controls and 3 caged in gaps, and 2 controls in the understory; for *T. bifoliolata*: 3 controls in
197 gaps; and for *T. korupensis*, 2 controls (gap and understory each).
198 In the third census (mid March 2009), each surviving seedling was checked and scored
199 for a vine climbing it (twined on the main stem or attached via tendrils = a vine colonization
200 event); if present, the vine(s) was clipped back—this was also done in the prior census—to
201 maintain the same growing conditions of control and caged seedlings (apart from their light and
202 herbivore exposure). This vine colonization of a seedling was observed just once in the
203 understory but 33 times in the gaps during this census. So, in the next (fourth) census (October
204 2009), vine occurrence was recorded on surviving seedlings *in canopy gaps only*.
205 To prevent temporal pseudo-replication, as well as possible cases of re-sprouting vines,
206 seedling responses were pooled over the latter two censuses (i.e., third + fourth). Thus, a given
207 seedling received an overall 'vine colonization event' score of "1" based on whether it had

hosted a vine at either time while still alive in 2009. Otherwise, a seedling was scored as "0". Occasionally, two vines (three cases in March 2009, all *M. bisulcata*), or even three vines (one case in March 2009, with *T. korupensis*) were found on the same seedling. Similarly, in October 2009, 5 of the 31vine-colonized seedlings at this time had two vines on them (three cases with *M. bisulcata*; plus one each for *T. bifoliolata* and *T. korupensis*). To simplify the analyses, all these cases were scored as a single vine colonization event. Vines were not taxonomically identified, hence they possibly included herbaceous in addition to any woody vine species.

From the March 2009 census, data were missing for one *M. bisulcata* seedling, a control. From the October 2009 census, 10 other seedlings (3 *M. bisulcata*, 2 *T. bifoliolata*, and 5 *T. korupensis*) also lacked data. These 11 seedlings were removed from the pooled data set before it was analyzed. Because insect herbivores substantially reduced the height and leaf numbers of faster-growing, less resistant *M. bisulcata* seedlings in gaps, whereas the corresponding growth rates of the more shade-tolerant *Tetraberlinia* species were negligibly affected after almost 2 yr (refer to Fig. 2d, h in Norghauer & Newbery 2013), the latter two species were grouped for the current analysis. Hereon I shall simply refer to *M. bisulcata* as '*Mb*', and the grouped *T. bifoliolata* and *T. korupensis* as '*Tbk*'.

EVALUATING VINE COLONIZATION IN GAPS, WITH AND WITHOUT HERBIVORES—Individual probability of vine colonization of the monitored seedlings, *in gaps* only, was modeled by logistic regression in a GLMM (generalized linear mixed model). This used the logit link function, an estimated dispersion parameter, and the Schall fitting method, with the fixed effects and variance components estimated by REML (restricted maximum likelihood), which sequentially reduces the weighted [or generalized] sums of squares (akin to a Type I SS strategy). The gap location of seedlings (= 'block') was an important random term, as vine

231 abundance varies strongly in space (Putz 1984; Dalling et al. 2012). The first fixed term was
232 light availability, expressed as a continuous explanatory variable: the percent transmittance of
233 PPFD (%PPFD) through the canopy incident above each seedling. This variable was transformed
234 and entered as $\log_{10}$ (%PPFD × 100), which normalized its distribution (Fig. S3), and also
235 centered (i.e., zero-weighted mean). The herbivory treatment (caged vs. control) was the next
236 fixed term, followed by its interaction with light availability.
237 Because of too-small sample sizes for robust logistic regression, the GLMM had to be
238 fitted separately for *Mb* and *Tbk* using their ungrouped binary data (Agresti 2007)—each
239 seedling had a single binary outcome for vine colonization over the observation period (Fig.
240 S3)—in GenStat v16.2 (VSN International Ltd. 2013). Importantly, for all fixed terms, Wald-
241 type *F* statistics were obtained for inference whose denominator (residual) degrees of freedom
242 (d.d.f.) were calculated using the method of Kenward & Roger (1997). This default correction in
243 Genstat (Payne 2015) helped to better control the Type 1 error rate in the GLMM; it is the same
244 Kenward–Roger approximation algorithm used for linear mixed models (LMMs) but applied to
245 the LMM on the transformed (link) scale at the last step of the underlying iterative algorithm.
246 Goodness-of-fit tests based on Pearson (χ^2) and deviance (G^2) statistics are not applicable
247 to ungrouped binary data (p. 147 in Agresti 2007). Instead, the average estimated probability of
248 vine colonization was obtained for 10 equal intervals of light availability, by summing the fitted
249 individual probabilities and dividing by the number of seedlings in a given interval (pp. 103-4 in
250 Agresti 2007). These were then visually compared to the observed sample proportions of vine
251 colonization. Additionally, conditional R^2 values are provided for the GLMMs (and for the
252 LMMs described below), as described in Nakagawa & Schielzeth (2013).

SEEDLINGS UNDER HERBIVORE PRESSURE IN GAPS—To explain the GLMM results, an attempt was made to the link susceptibility to folivory and vine colonization**.** To directly gauge the activity of insect herbivores, only unprotected seedlings in gaps (i.e., control group) were investigated further (since the caged treatment prevented insect attacks). Specifically, the proportion of extant leaves on a seedling with signs of insect chewing was examined, which I had recorded on all live experimental tree seedlings in October 2009 (full details on this measurement is described in Norghauer & Newbery 2013). This included all but one control seedling with a vine colonization event. To determine how this incidence of leaf herbivory differed between a seedling's identity (*Mb* vs. *Tbk*), and whether or not it experienced vine colonization (1 vs. 0 score = yes vs. no), a linear mixed model (LMM) was used: light availability ($\log_{10}$ [%PPFD × 100]) was entered first, with gap as the blocking (random) term.

CORROBORATING HOST TREE STATURE IMPORTANCE FOR VINE COLONIZATION IN GAPS—In an ad-hoc explanatory analysis, a three-way crossed factorial LMM tested whether vine-colonized seedlings that were taller—that is, seedling height was the response variable—than those lacking a vine (yes vs. no) depended on host species identity (*Mb* vs. *Tbk*) as well as exposure to insects (caged vs. control; i.e., a significant 2nd order interaction). Inclusion of host tree height as a covariate in the earlier GLMM was not justified because it is confounded with light availability and the herbivory treatment (it was known *a priori* that insects suppressed *Mb*'s growth in height and leaf numbers in gaps; see Norghauer & Newbery 2013). Using height as a proxy for plant stature is justified given the strong correlations between final heights, leaf numbers, and basal stem diameters of the three tree species (nine Pearson *r*-values = 0.73–0.92, all *P*-values < 0.001). Both this LMM and the one described before, for leaf herbivory, were fitted well (had normal residuals and homogeneity of variance).

RESULTS

VINES IN THE UNDERSTORY VERSUS GAPS—In the gap habitat 33 and 31 tree seedlings had at least one vine on them in March and October 2009, respectively. By contrast, in the forest understory just one case was recorded out of 257 live seedlings surveyed in March 2009. The following results thus apply to the gap sample only.

OVERALL VINE COLONIZATION FREQUENCIES IN GAPS—When the data from gaps in both censuses were tallied and combined, a total of 51 out 315 scored seedlings were vine-colonized (as 13 seedlings hosted vines in both censuses). Remarkably, the overall proportion of seedlings—i.e., irrespective of the herbivory treatment—hosting a vine was identical between the two tree species groups, at 0.16 (30/185 for *Mb* and 21/130 for *Tbk*; Fig. 1A). Ignoring continuous light availability, an association between herbivory and vine colonization of *Mb* was plausible (2×2 contingency table test, $\chi^2 = 3.25$, $P = 0.072$) but clearly not for *Tbk* ($\chi^2 = 0.51$, $P = 0.475$; Fig. 1A). However, relatively more of the latter species (22.6%) had vines than did the former (12.7%) under normal gap conditions (i.e., when exposed to insects), while this pattern was reversed, albeit slightly less pronounced, when seedlings were protected from herbivore pressure (*Mb*: 26.3% and *Tbk*: 16.1%; Fig. 1A).

VINE COLONIZATION WITH HIGHER LIGHT IN GAPS—For *Mb* seedlings, light availability influenced vine colonization differently whether they were accessible to insects or not (GLMM, PPFD × treatment interaction, Wald-type F statistic$_{1, 167.3} = 11.22$, $P = 0.001$; Table S4). When herbivores had access to seedlings, as they would naturally, vine colonization was generally low across light levels, with some bimodality indicated (at log %PPFD = ~2.4 and ≥ 3.1; Fig. 2A); however, when protected from herbivores the better-illuminated seedlings increasingly became more susceptible to vines (Fig. 2B). Vine colonization of control seedlings apparently peaked at two

299 levels of light availability, whose fit was improved by adding a quadratic light term to the
300 GLMM (AIC reduced by 9.35; Table S4) as initially suggested by their binary data distributions
301 (Fig. S3). Some gap locations had greater vine colonization of *Mb* seedlings than did others (the
302 block term's variance component was 18% larger than its standard error), but this spatial effect
303 was negligible for *Tbk*.

304 For the *Tbk* seedlings, the light environment only had a slightly positive effect on their
305 colonization by vines (PPFD term, Wald-type $F_{1, 126.0} = 3.40$, $P = 0.064$; Table S4), while
306 exposure to insect herbivores clearly did not change their susceptibility to it ($P = 0.683$ and $P =$
307 0.283 for treatment and interaction terms, respectively). Unlike for *Mb*, the apparent peak in
308 colonization at higher light availability (log %PPFD = ~2.8–3.0; Fig. 2C) in the *Tbk* control
309 seedlings could not be accommodated by a quadratic term (AIC increased from 404.62 to
310 437.56, model not shown). Evidently, the ability of the tested ecological factors (light
311 availability, insect herbivores) to jointly predict vine colonization events was more reliable for
312 Mb (its GLMM's goodness-of-fit was more acceptable than *Tbk*'s). While good predictive power
313 was obtained for the caged *Mb* seedlings (Fig. 2B), in the other cases (Fig. 2A, C, D) the fit was
314 poor at several light intervals. Importantly, in the absence of insect herbivores, of those seedlings
315 receiving the most light in gaps 60–80% of *Mb* were found colonized by a vine (Fig. 2B),
316 slightly more than twice that of *Tbk* (Fig. 2D).

317 LINKING FOLIVORY TO VINE COLONIZATION IN GAPS—The unprotected (control) seedlings
318 colonized by a vine had a lower proportion of their leaves damaged by insects (adjusted mean =
319 0.60) than counterparts free of vines (= 0.48; LMM, vine colonization main term, Wald-type $F_{1,}$
320 $_{109.2} = 8.51$, $P = 0.004$). This difference did not depend on their species identity (vine × species
321 interaction term, $P = 0.211$; Fig. 3), after first accounting for effects of light availability (light

term, Wald-type $F_{1, 114.0} = 1.85$, $P = 0.177$) and the tree species (*a priori* known) differences in susceptibility to herbivory (species term, Wald-type $F_{1, 104.4} = 4.68$ $P = 0.033$). In this LMM, when a plant's height was substituted for the light it received in a gap—including both predictors in a single model violated its assumptions, since light had a strong positive effect on height (Norghauer & Newbery 2013, 2014)—the taller control seedlings generally had experienced a lower incidence of insect herbivory (LMM, seedling height covariate, Wald-type $F_{1, 114.0} = 7.39$, $P = 0.008$), as did the vine-colonized seedlings (Wald-type $F_{1, 108.8} = 6.20$, $P = 0.014$), irrespective of species identity (the interaction remained insignificant, $P = 0.320$).

HOST STATURE WHEN VINE COLONIZED IN GAPS—As Fig. 1B shows, the herbivore-exposed seedlings of *Mb* were similar in height whether vine-colonized or not, but when released from herbivore pressure in gaps the caged seedlings of this fast-growing species that hosted a vine were almost twice as tall as those not colonized. Notably, this pattern was reversed for *Tbk*, in that its control seedlings colonized by a vine were significantly greater in height than those found vine free, whereas when caged this size-difference effect weakened (LMM, three-way interaction term shown in Fig. 1B; Table S5).

DISCUSSION

We need more field studies that manipulate plant exposure to insects to determine their influence upon vine colonization of seedlings and saplings in forests. The experimental results here suggest insects could differentially alter vine colonization of dominant trees species with contrasting life histories. This mediating effect, presumably from herbivory to seedlings or vines, or both, further depended on microsite light availability for the dominant, long-lived grove-forming tree *M. bisulcata*, a large fast-growing and light-demanding species that has been studied at Korup National Park since 1991 (Newbery et al. 1998, 2013).

345 The identical overall colonization between host species groups in gaps (16.1%) across
346 ~80 ha of Korup forest would suggest these vines, as a group, behaved as generalist structural
347 parasites (Putz 1984; Babweteera et al. 2000; recently Visser et al. 2018a). Nevertheless, rates of
348 vine colonization likely change with tree ontogeny; for example, trees of ≥ 20 cm stem diameter
349 in Panama had woody vine infestations that varied strongly among species and with their shade-
350 tolerance (Visser et al. 2018b). By contrast, in the understory at Korup, the experiment's newly
351 established *M. bisulcata* and *Tetraberlinia* seedlings barely grew in height (Norghauer &
352 Newbery 2013), thus limiting their availability as suitable support hosts (Putz 1984). However,
353 owing to their shade-tolerance, over a longer time frame the better survival of *T. bifoliolata* and
354 *T. korupensis* seedlings (Newbery et al. 2006) creates a combined sapling bank that greatly
355 exceeds that of *M. bisulcata* (Newbery et al. 1998). This represents a stable supply of potential
356 hosts for vine species able to tolerate shaded conditions once the gaps closed up.
357 Insects suppressed vine colonization of *M. bisulcata*, especially of its well-illuminated
358 hosts (Fig. 2A, B), but not so for *Tbk*, whose seedlings were nonetheless more prone to vines
359 when exposed to these herbivores (Fig. 1A). Two explanatory mechanisms related to species
360 differences in host size and leaf traits are plausible. First, by keeping *M. bisulcata* seedlings
361 small in height but not *Tetraberlinia* spp. (Fig. 1B), insect herbivores reduced the likelihood of
362 vines encountering hosts in gaps by chance alone, given their strong co-occurrence there (e.g.,
363 Blick & Burns 2011). But it is not at all inconceivable that vines may have searched for a larger-
364 sized host plant near them, by growing away from the light, and towards the tallest seedlings
365 casting the most shade through a form of skototropism (Strong & Ray 1977), given the very
366 contrasting light-dependent patterns of Fig. 2A, B, and the fact that, overall, relatively more
367 *Tetraberlinia* controls were colonized than smaller-sized *M. bisulcata* counterparts (Fig. 1A). As

368 argued recently by Gianoli (2015), a preference for taller hosts may confer a greater fitness
369 currency to vines, in the parlance of optimal foraging theory, especially if they are capable of
370 cue-oriented growth (e.g., skototropism) among neighboring plants to find favorable supports.
371 Second, it may be that vines failed to colonize well-lit *M. bisulcata* (in Fig. 2A) because
372 they too were heavily eaten by insects in gaps—as predicted by the plant vigor hypothesis (Price
373 1991; e.g., Hough-Goldtsein & LaCoss 2012)—or due to associational susceptibility (Gianoli
374 2015) with this host tree species and its thin, palatable leaves (Norghauer & Newbery 2014).
375 Conversely, in addition to host size, vines might also have benefited from associational
376 resistance with the more herbivore-resistant (less palatable) *Tetraberlinia bifoliolata* and *T.*
377 *korupensis* leaves (Norghauer et al. 2014). For example, in a temperate South American forest,
378 the proportion of leaf area damaged in *Vicia nigricans* on one shrub species was double that on
379 its other host (Sasal & Suarez 2011). It is less clear whether or not vines may confer
380 associational resistance to juvenile host trees, as suggested by Piiroinen et al. (2013), who
381 reported the leaf area eaten (%) of the pioneer *Neoboutonia macrocalyx* was lower on its
382 seedlings with fewer vines on them in gaps of post-logged conifer plantations in Kibale National
383 Park (Uganda). No such evidence was found at Korup, where tree seedlings generally incurred
384 more frequent bouts of herbivory when hosting a vine in canopy gaps (Fig. 3), pointing instead to
385 associational susceptibility. Such associational effects for herbivory between co-occurring plant
386 species in patchy resource-rich habitats deserve more field study (Hambäck et al. 2014) and may
387 prove crucial for predicting vine-tree interactions in tropical forest communities.
388 A third factor possibly relevant to vine colonization is leaf trait morphology of host
389 plants. In re-analyzing the two *Tetraberlinia* species in separate GLMMs (Table S6), light
390 availability strongly promoted vine colonization of *T. bifoliolata* (light term, $P = 0.004$) which

391 has a leaf consisting of two large, lobed leaflets (bifoliate). However, for *T. korupensis*, whose
392 leaves are morphologically very similar to *M. bisulcata* (simply pinnate, with many opposite
393 leaflets) but chemically better defended, exposure to insects only interacted to some extent with
394 host's seedling light environment (PPFD × treatment interaction, $P = 0.160$) Although this post-
395 hoc investigation had low statistical power ($n < 100$ per GLMM, further justifying the *Tbk*
396 grouping before), it points to leaf morphological differences among species perhaps being
397 important for influencing vine-insect-tree interactions in canopy-disturbed areas. Plants with
398 pinnate compound leaves, whose leaflets are easily shed (from biotic or abiotic damage), may
399 have a lower leaf area index (LAI) than those with thicker, non-pinnate leaves, making the latter
400 species more liable to be colonized if vines gravitated towards larger-sized host seedlings in gaps
401 using LAI as a primary search cue.
402 This study has several caveats, whose consideration illustrates the logistical difficulty
403 involved in conducting a "clean experiment" in a tropical rainforest. First, hosts in the control
404 treatment, with its mesh rooftop and open sides, could have been accessible to more vines if
405 these foraged more than ~0.5 m across the ground and came from dispersed seeds >1 mm × 4
406 mm in size (= mesh opening) that landed nearby. Yet, by the same token, a vine established near
407 a control seedling could move further away from it and colonize a different host, whereas in a
408 caged treatment its mesh sides limited both aspects of vine behavior. Second, by enlarging a
409 cage, relatively more germinating or established vines could have been inadvertently "trapped"
410 inside it with the host seedling. Third, both herbivory treatments were supported by bamboo
411 posts, which being bare for the control seedlings may have lured vines away from them, while
412 those affixed with mesh side walls could have provided scaffolding for vines to climb inside the
413 cages. The net effects of these experimental artifacts on the results are unknown. Vegetation

414 cover around the seedlings was systematically assessed in November 2009 and found to be
415 similar at two strata between cages and controls in gaps (Norghauer & Newbery 2013). Another
416 caveat is that the mesh-netting also excluded potential mammalian herbivores; at Korup they
417 apparently neither grazed nor browsed the studied tree seedlings, but rodents can lethally sever
418 their stems near the base, especially those of *M. bisulcata* (Norghauer et al. 2016). Hopefully,
419 highlighting these caveats may better prepare ecologists intending to experimentally investigate
420 vine colonization of young trees. Alternatively, one could try to chemically exclude insects from
421 host seedlings, but the efficacy of this is questionable in gaps open directly to rain, especially in
422 very wet lowland forests like Korup, and it may have other unintended consequences too.
423 Compared with *M. bisulcata*, relatively higher vine colonization on the *Tetraberlinia* spp.
424 under normal forest conditions (i.e., with exposure to insects = control) may lead to recurring
425 higher liana loads on these shade-tolerant, slower-growing trees as they ascend to the canopy and
426 mature. Hence, these findings appear consistent with the reportedly stronger direct impacts of
427 vines on shade-tolerant tree species (e.g., Schnitzer & Carson 2010). Nonetheless, *M. bisulcata*
428 seedlings were at risk of colonization even at low light in gaps; over time, a survivorship bias
429 towards those being vine-free may occur if vine loading reduces survival rates of faster-growing
430 species (Visser et al. 2018a), especially following canopy gap closure. But whether or not this
431 vine interference can also reduce *M. bisulcata*'s population-wide sapling and adult recruitment
432 rates is unknown, depending on the proportion of stems colonized and host tolerance to vine
433 infestations (Visser et al. 2018b). If it does, this may contribute cryptically to the currently poor
434 regeneration of *M. bisulcata* groves at Korup (Newbery et al. 1998, 2006). However, should the
435 better-illuminated *M. bisulcata* juveniles be able to tolerate interference from vines, or soon shed
436 them through ontogeny—particularly via its remarkably fast growth in 10–50-cm stem diameter

437 size classes (Newbery et al. 2013)—then it is plausible this species recruitment may benefit from
438 conditions that also favor vine recruitment. Conversely, vine colonization likely has little
439 immediate impact on the persistence of *Tetraberlinia* seedlings and saplings, since shade-tolerant
440 species can also better tolerate hosting vines (Visser et al. 2018b) after gap closure. Yet,
441 ontogenic shifts in host tolerance to vine infestation should not be discounted either: for
442 example, among bole- and adult-sized trees (>20 cm stem diameter), more of *T. bifoliolata*, and
443 *T. korupensis* to a lesser extent, are found vine-laden than *M. bisulcata* (Norghauer, *pers.*
444 *observations*) and this biotic stress may contribute to the higher *Tetraberlinia* spp. mortality rates
445 at Korup (Newbery et al. 2013). Woody wines are thought to compete directly with juvenile trees
446 for belowground resources (Schnitzer et al. 2005; Toledo-Aceves & Swaine 2008b), especially
447 for water during dry periods in seasonal forests (Schnitzer & Bongers 2011; Alvarez-Cansino et
448 al. 2015). It is tempting to speculate that vine colonization and interference with shade-tolerant
449 competitors of *M. bisulcata*, such as the two *Tetraberlinia* species (and perhaps others), would
450 strengthen during large-scale regional droughts. These climatic events, as argued by Newbery et
451 al. (2013), are necessary for *M. bisulcata* grove maintenance at Korup, and they might also
452 reduce forest-wide insect herbivore abundance and pressure, further favoring *M. bisulcata*'s
453 regeneration.

454 Almost all the vines observed on seedlings/saplings had wound themselves on main stem
455 (twining) or latched laterally using tendrils. No attempt was made to quantify either climbing
456 habit, nor were the vines taxonomically identified, so it is unknown if any were perhaps
457 herbaceous. Currently, it is also unknown which insect taxa feed on vines in gaps at Korup.
458 Future studies that manipulate exposure to herbivores, whether of invertebrates or vertebrates,
459 should consider recording the habits of vines on young trees using very large samples ($n > 200$)

of multiple host species along the fast-slow growth spectrum. To my knowledge, a systematic *in situ* community-level study of herbivory of both vines and their host trees has yet to be done.

To conclude, the results demonstrated how herbivores could interact with canopy disturbances to differentially shape vine colonization events on tree hosts across space, which could broaden our understanding of forest regeneration dynamics. Vines prefer to colonize taller hosts, to more quickly climb or be carried upward, but insects interact with light to mediate this process in gaps, by stunting the vertical growth of faster-growing individuals of more palatable light-demanding species. This causes vine colonization rates at higher light levels to become more similar between slow and fast-growing tree species. Since both vines and gaps are fundamental features of tropical forests, these findings from Korup may apply to other co-existing tree species on the fast-slow growth rate spectrum associated with shade-tolerance as juveniles. In particular, it would be pertinent to know how changes in soil fertility and seasonality influence vine colonization and to conduct long-term studies of its impact on tree population dynamics, while the relative importance of mycorrhizal associations of co-occurring vine and tree species seems ripe for study. Investigations of vine-tree-herbivore interactions may also be timely for understanding vines' behavior (Gianoli 2015) and their ongoing abundance and biomass increases in tropical America but not Africa (Schnitzer & Bongers 2011). For these reasons, well-replicated inter-continental experiments may prove particularly insightful.

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DATA AVAILABLITY

The data used in this study are archived at the Dryad Digital Repository:

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FIGURE LEGENDS

FIGURE 1. (A) Tallies of overall vine colonization events of tree seedlings protected from (caged) and exposed to insect herbivores (control) in rainforest gaps at Korup, Cameroon, and **(B)** their corresponding mean (± SE) heights of surviving seedlings in November 2009. **Mb:** *Microberlinia bisulcata*, **Tbk:** *Tetraberlinia bifoliolata* and *T. korupensis*. Seedling height was $\log_{10}$-transformed in a linear mixed model (LMM, Table S5): the 2nd-order interaction term of host species group × herbivory treatment × vine colonization was significant ($F_{1,\ 238.4} = 7.79$, $P = 0.006$). Different letters indicate statistically different means, based on planned LSD tests (5% alpha level). The mean %PPFD (± SE) of the four groups of seedlings, from left to right, was 5.39 ± 0.40, 5.59 ± 0.45, 5.59 ± 0.35, and 4.91 ± 0.35. (%PPFD is the percentage of photosynthetic photon flux density transmitted through the forest canopy reaching a seedling.) In (B), the samples size per bar, going from left to right: 9, 50, 12, 48, 20, 73, 9, and 56 seedlings. The goodness-of-fit for this LMM, following Nakagawa & Schielzeth (2013), had a conditional $R^2 = 0.566$.

FIGURE 2. Observed and fitted proportions of tree seedlings colonized by a vine in rainforest gaps at Korup (Cameroon) as a function of light resource availability (x-axis), when exposed to insect herbivores **(A, C)** or protected from them by mesh-netting cages **(B, D)** for the two species identity groups (**Mb**: *Microberlinia bisulcata*, **Tbk**: *Tetraberlinia bifoliolata* and *T. korupensis* grouped). Observed proportions (y-axis) for each light interval are shown. Curvature in the data of **(A)** was accommodated by a quadratic term for light availability in the GLMM (Table S4); however, in **(C),** adding a quadratic term did not significantly improve the fitted model. "%PPFD": percentage of photosynthetic photon flux density transmitted through the forest canopy reaching a seedling. Sample sizes (total n = 315) per light interval (left to right): **(A)** 5,

613 10, 12, 6, 19, 14, 11, 3, 3, and 6; **(B)** 7, 5, 12, 9, 17, 18, 11, 6, 7 and 4; **(C)** 1, 8, 10, 7, 6, 14, 7, 5,
614 2, and 5; **(D)** 3, 4, 11, 13, 11, 10, 6, 3, 1, and 3. The goodness-of-fit of each GLMM, following
615 Nakagawa & Schielzeth (2013), had conditional R^2 values of 0.335 and 0.256 for *Mb* and *Tbk*,
616 respectively.
617 **FIGURE 3.** Boxplots showing the incidence of insect herbivory on leaves of unprotected (i.e.,
618 control group) tree seedlings with and without vines, in rainforest gaps at Korup (Cameroon).
619 Data are shown for two species identity groups (**Mb**: *Microberlinia bisulcata*, **Tbk**:
620 *Tetraberlinia bifoliolata* and *T. korupensis* grouped). Group sample sizes, from left to right, were
621 n = 50, 9, 48, and 12 individual seedlings, for which corresponding raw (unadjusted) means (±
622 SE) were 0.55 ± 0.033, 0.48 ± 0.031, 0.65 ± 0.031, and 0.43 ± 0.073. These were analyzed in a
623 linear mixed model (LMM) able to accommodate the unbalanced sample sizes (in which the
624 means were first adjusted for light availability [as a centered covariate] to individual seedlings).
625 The goodness-of-fit for that LMM, following Nakagawa & Schielzeth (2013), had a conditional
626 $R^2 = 0.304$.
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636 **Figure 1**

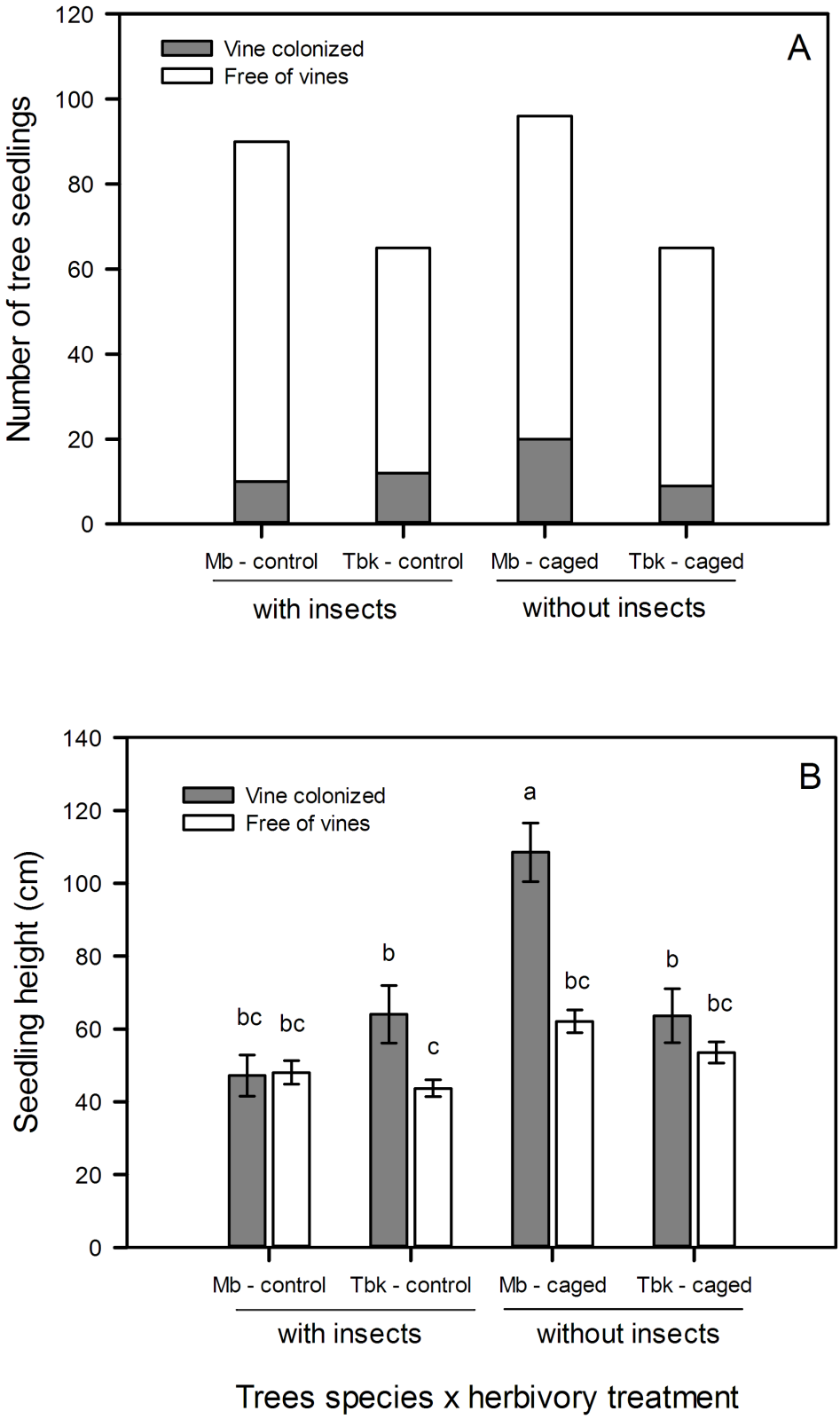

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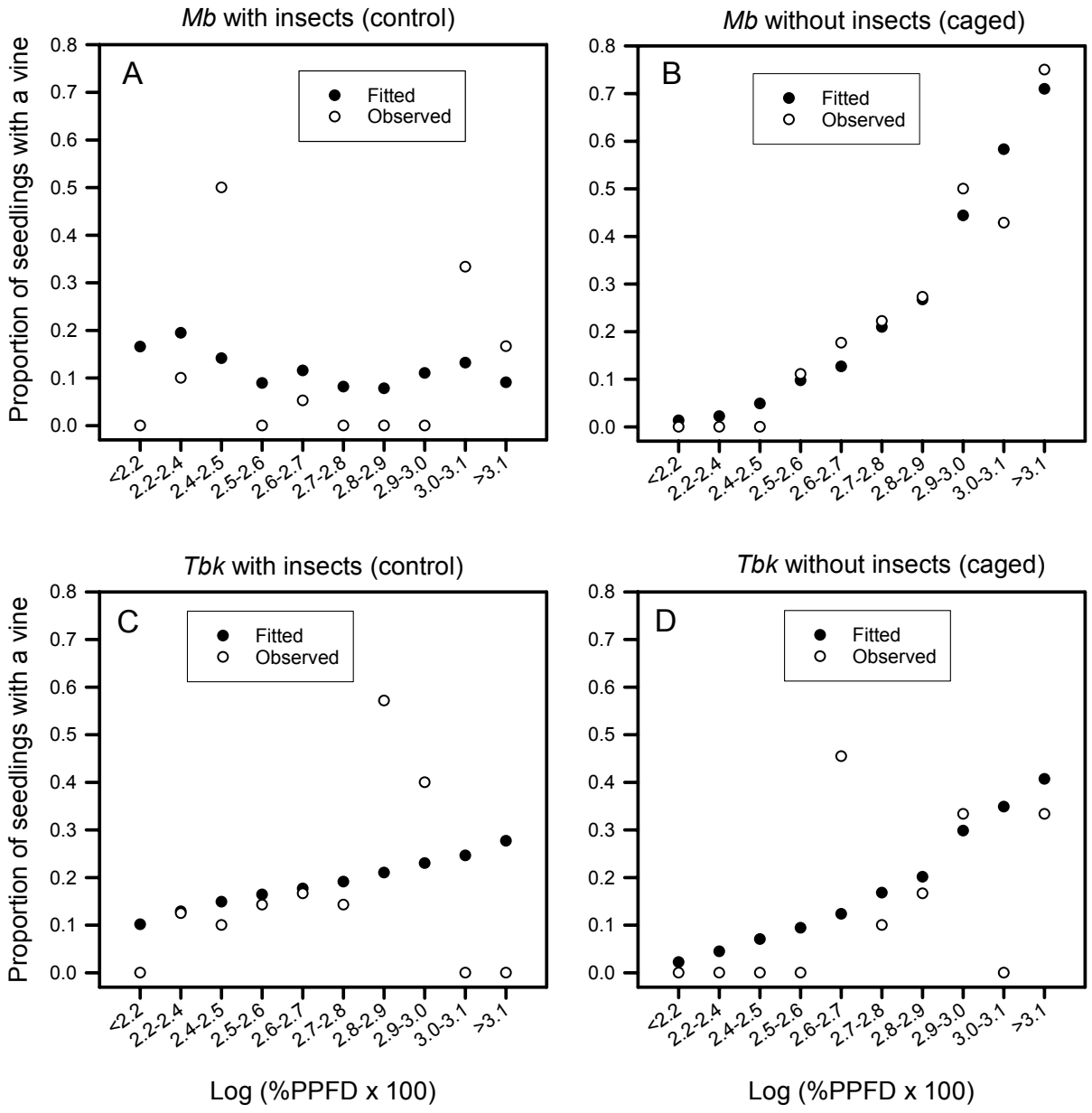
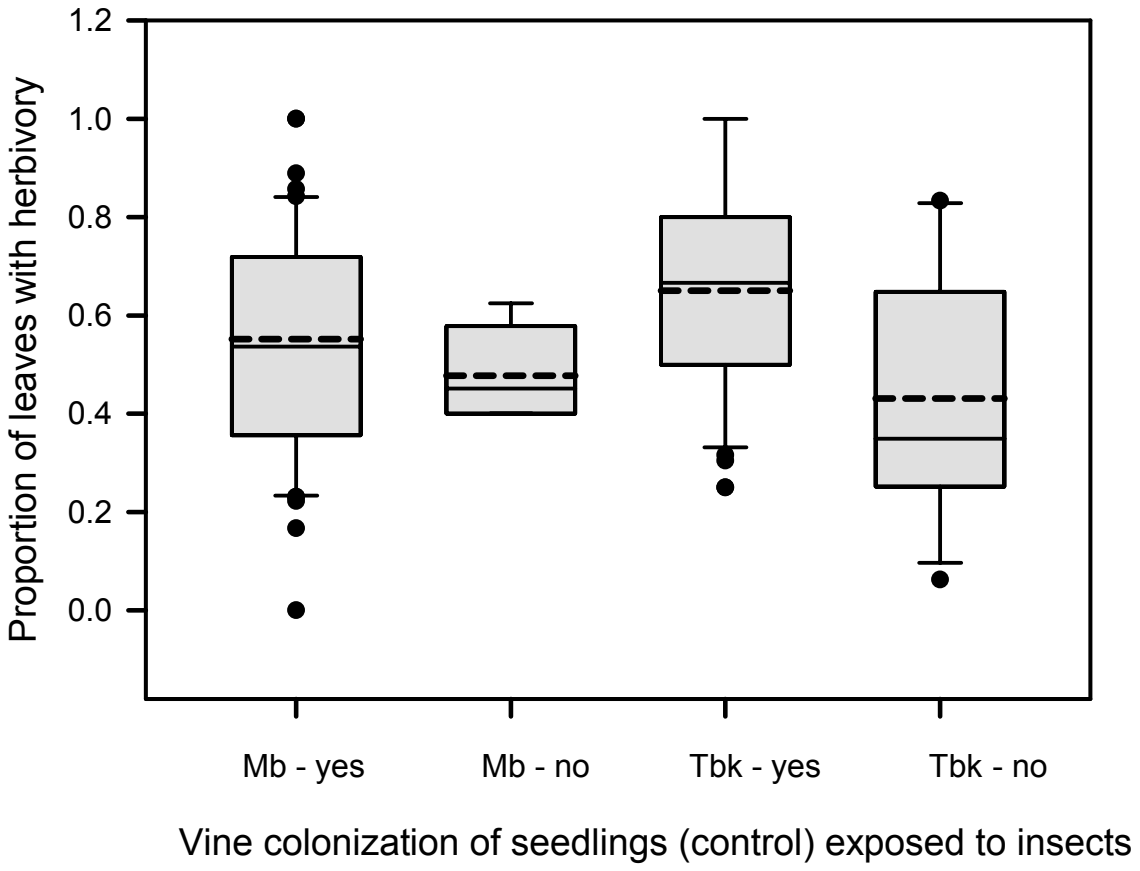
Figure 2


Mb with insects (control)
Mb without insects (caged)
Tbk with insects (control)
Tbk without insects (caged)
A
B
C
D
Fitted
Observed
Proportion of seedlings with a vine
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
<2.2
2.2-2.4
2.4-2.5
2.5-2.6
2.6-2.7
2.7-2.8
2.8-2.9
2.9-3.0
3.0-3.1
>3.1
Log (%PPFD x 100)

645 **Figure 3**



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SUPPLEMENTARY INFORMATION

TABLE S1. Initial sample sizes and heights of the tree seedlings used the field experiment.

FIGURE S2. Distributions of PPFD values before and after log transformation.

FIGURE S3. Scatterplots of binary data used in the GLMM of vine colonization.

TABLE S4. GLMM results for vine colonization of tree seedlings in canopy gaps.

TABLE S5. LMM results for tree seedling heights.

TABLE S6. Separate GLMMs for vine colonization of the two *Tetraberlinia* species.

Table S1

Starting samples sizes of newly established seedlings (n = 664 in total) used in the insect herbivore-exclusion experiment carried out at Korup National Park, Cameroon. Canopy gap and understory locations were paired, to form a spatial block. Number of locations (gap or understory) were 34, 18, and 10 for *Microberlinia bisulcata*, *Tetraberlinia bifoliolata*, and *T. korupensis*, respectively. But since one, two, or all three species co-occurred at a given location, the total block number summed to 41. In parentheses are the ranges in initial seedling heights. Mean heights were not significantly different among the 12 groups (Norghauer & Newbery 2013).

	M. bisulcata	*T. bifoliolata*	*T. korupensis*
Gap locations			
control	97 (13.5–30.3 cm)	43 (13.7–25.6 cm)	26 (19.4–29.0 cm)
caged	97 (13.5–32.2 cm)	43 (14.3–24.8 cm)	26 (13.5–32.2 cm)
Understory locations			
control	97 (16.0–26.5 cm)	43 (17.1–27.3 cm)	26 (14.7–25.5 cm)
caged	97 (14.5–24.5 cm)	43 (16.3–25.1 cm)	26 (17.5–26.0 cm)
Totals	**388**	**172**	**104**

Figure S2

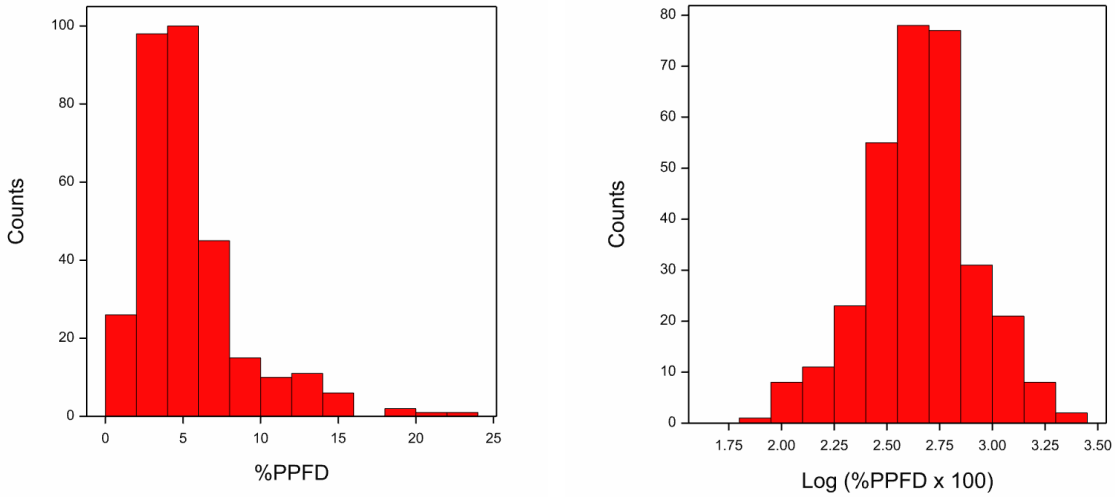
Counts
%PPFD
0
5
10
15
20
25
0
20
40
60
80
100
Counts
Log (%PPFD x 100)
1.75
2.00
2.25
2.50
2.75
3.00
3.25
3.50
0
10
20
30
40
50
60
70
80

Figure S3

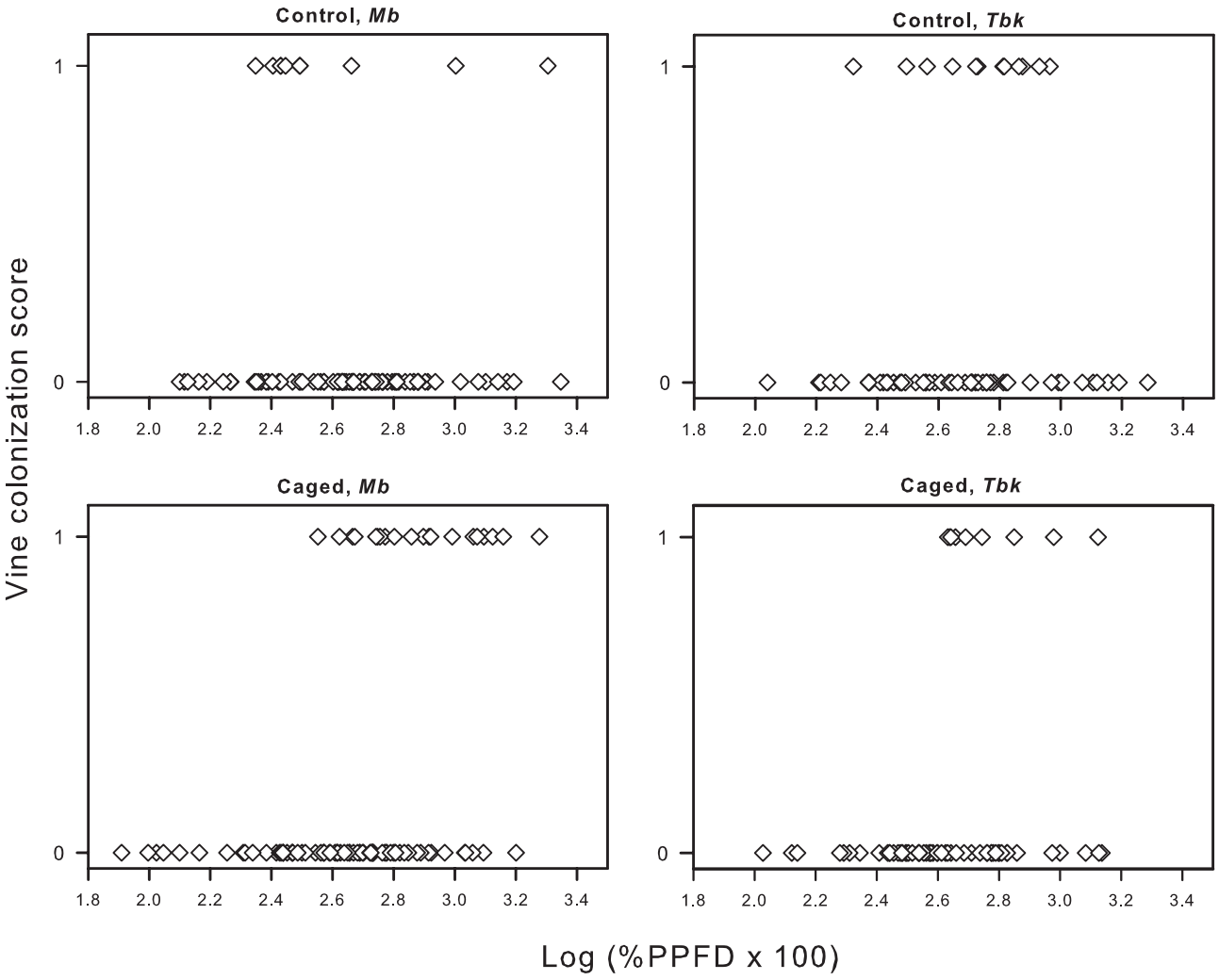
Control, Mb
Control, Tbk
Caged, Mb
Caged, Tbk
Vine colonization score
Log (%PPFD x 100)
0
1
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
3.4

Table S4

The GLMMs testing the fixed effects of light availability (log [%PPFD × 100] = 'PPFD'), and insect herbivory treatment (control vs. caged) on the probability of vine colonization of rainforest seedlings in canopy gaps at Korup, Cameroon. In the GLMM for *Microberlinia bisulcata* (*Mb*) as hosts, including a quadratic term ('$PPFD^2$') improved the model fit (i.e., reduced its AIC value from 600.55 to 591.20; both models shown), whereas it did not for the GLMM (not shown) using the pooled sample of *Tetraberlinia bifoliolata* and *T. korupensis* (*Tbk*). Noteworthy effects of ecological interest are in bold.

	Coefficient (β)	SE*	n.d.f.	Wald (*F*-statistic)	d.d.f.	*P*-value
Mb†						
Base GLMM:						
constant	–2.230	0.365				
PPFD	**–1.055**	**1.253**	**1**	**7.80**	**159.7**	**0.006**
treatment	0.6948	0.440	1	2.01	160.7	0.158
PPFD × treatment	**6.362**	**1.8145**	**1**	**12.29**	**177.9**	**< 0.001**
GLMM with a quadratic term						
constant	–2.243	0.361				
PPFD	**–7.727**	**13.318**	**1**	**7.22**	**177.0**	**0.008**
$PPFD^2$	1.251	2.494	1	1.86	176.4	0.174
treatment	**0.7100**	**0.4355**	**1**	**2.89**	**159.7**	**0.091**
PPFD × treatment	**6.075**	**1.814**	**1**	**11.22**	**167.3**	**0.001**
Tbk‡						
constant	–1.450	0.316				
PPFD	**1.064**	**1.233**	**1**	**3.40**	**126.0**	**0.064**
treatment	–0.259	0.484	1	0.26	126.0	0.613
PPFD × treatment	2.240	2.077	1	1.16	126.0	0.283

* The standard error (SE) of differences is given for the categorical and interaction terms

† Base model, dispersion estimate = 0.804, SE = 0.0908, with a conditional R^2 = 0.381 (following Nakagawa & Schielzeth 2013); Quadratic model (Fig. 2AB), dispersion = 0.782, SE = 0.0886

‡ Dispersion estimate = 0.964, SE = 0.1214

Table S5

The LMM used to examine how the final height of surviving tree seedlings was related to their species identity group (*Microberlinia bisulcata* vs. *Tetraberlinia bifoliolata/korupensis*), insect herbivory treatment (control vs. caged), and experience of vine colonization (yes vs. no; "vinecol") at Korup, Cameroon. 'block' = the canopy gap in which the individual seedlings grew. Noteworthy effects of ecological interest are in bold. The seedling heights were log-transformed to normalize the residuals.

Fixed terms	n.d.f.	Wald (*F*-statistic)	d.d.f.	*P* value
species	**1**	**23.24**	**260.2**	**< 0.001**
treatment	**1**	**54.08**	**236.1**	**< 0.001**
vinecol	**1**	**31.04**	**244.8**	**< 0.001**
species × treatment	**1**	**9.24**	**235.5**	**0.003**
species × vinecol	1	0.00	244.2	0.960
treatment × vinecol	1	2.26	239.7	0.134
treatment × species × vinecol	**1**	**8.24**	**237.8**	**0.004**
Random term	Estimate	SE		
block	0.0156	0.00146		

Table S6

Two ad-hoc GLMMs testing the fixed effects of light availability (log [%PPFD × 100] = 'PPFD'), and insect herbivory treatment (control vs. caged) on the probability of vine colonization of the two *Tetraberlinia* species' seedlings in canopy gaps at Korup, Cameroon. Noteworthy effects of ecological interest are in bold.

	Coefficient (β)	SE*	n.d.f.	Wald (*F*-statistic)	d.d.f.	*P*-value
T. bifoliolata†						
constant	–1.508	0.532				
PPFD	**4.805**	**1.951**	**1**	**8.94**	**54.1**	**0.004**
treatment	–0.5294	0.523	1	1.01	62.2	0.319
PPFD × treatment	1.176	2.478	1	0.23	62.7	0.637
T. korupensis‡						
constant	–1.377	0.494				
PPFD	0.582	1.782	1	1.30	46.0	0.326
treatment	–0.0255	0.770	1	0.02	46.0	0.991
PPFD × treatment	**6.263**	**4.383**	**1**	**2.84**	**46.0**	**0.160**

* The standard error (SE) of differences is given for the categorical and interaction terms

† Dispersion estimate = 0.565, SE = 0.1032; conditional R^2 = 0.439, following Nakagawa & Schielzeth (2013)

‡ Dispersion estimate = 0.974, SE = 0.2030; conditional R^2 = 0.183, following Nakagawa & Schielzeth (2013)